Original investigation

Assessment of habitat quality for four small mammal species of the Monte Desert, Argentina

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Abstract

In the temperate desert of Argentina, the combined action of climatic and anthropogenic factors has contributed to the formation of a highly heterogeneous landscape. In the central region of the Monte desert, four small mammal species (*Eligmodontia typus*, *Calomys musculinus*, *Akodon molinae* and *Graomys griseoflavus*) coexist and show different habitat uses in response to spatial variability. Three main habitat types are present in the region: mesquite forest, the creosotebush community and sand dunes. These habitat types are present also in the surrounding grazing area.

The objective of this study was to determine habitat quality for these species in a protected area (Reserve MaB Ñacuñán) and in the adjacent grazed area. For each species we estimated demographic parameters that are highly correlated to fitness in each habitat, and for both treatments (protected and grazed).

We found that the protected area offered a higher quality habitat than the grazed area for all species, but principally *A. molinae* and *G. griseoflavus*. At a local scale, we found that *A. molinae* and *C. musculinus* clearly showed higher fitness in the more complex habitats as the creosotebush community and the mesquite forest. In contrast, for *E. typus*, open and simplest patches, such as sand dunes, were optimal for its survival and reproduction.

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Introduction

Habitat selection theory suggests that individuals occupy habitats where their fitness and survival are optimal (Fretwell and Lucas 1970; Fretwell 1972). According to this, population densities should reflect higher-quality habitats. However, several authors agree that density could be a misleading indicator of habitat quality (Van Horne 1983; Winker et al. 1995; Pulliam 2000). Poor habitats sometimes contain high densities of individuals by immigration from better habitats (Van Horne 1983; Bissonette and Broekhuizen 1995; Fryxell 2001).

Recently, other parameters have been added to density in order to assess habitat quality, by comparing survival, reproduction, adult sex ratios, movements of individuals, and resource availability among areas with different characteristics (Lidicker 1995; Loeb 1999; Wheatley et al. 2002). In better habitats, sex ratio can frequently favour females, especially during the breeding season (Lidicker 1995). Differential sex distribution

with female dominance in more favourable habitats is a behaviour that maximises reproductive effort and survival of the young (Bowers and Smith 1979). Adult survival and proportion of reproductive females may also be higher in better patches (Diffendorfer 1998; Loeb 1999). Furthermore, favourable habitats could be identified by a higher proportion of adults than juveniles, since dominant adults can expulse juveniles from optimal to suboptimal habitats by intraspecific competition (Van Horne 1982).

In the central region of the Monte Desert, four murid rodent species coexist and exhibit different habitat uses (Corbalán and Ojeda 2004) in response to spatial variability, i.e. their densities change according to habitat heterogeneity. Vegetative cover (which provides refuge) and abilities to escape from predators are keys in the spatial organisation of the community (Taraborelli et al. 2003; Corbalán and Ojeda 2004). *Eligmodontia typus* is efficient in avoiding predators due to its morphological and behavioural attributes (elongated hind legs, erratic escape behaviour, and hairy cushions on the soles of its feet), being the dominant species in open areas such as sand dunes. *Graomys griseoflavus* also has antipredator peculiarities, such as a bicoloured long tail with a tuft at the end, and displays abrupt and quick changes of direction when escaping. It is able to exploit different habitats but prefers those dominated by trees of *Prosopis flexuosa*. *Akodon molinae* and *Calomys musculinus*, lacking antipredator morphologies, are more dependent on plant cover and more abundant in a creosotebush community (Taraborelli et al. 2003; Corbalán and Ojeda 2004).

The aim of the present study is to determine whether species density might reflect habitat quality for these four murid rodents when reproductive parameters, sex and age rates, and survival are incorporated in the analysis.

Material and methods

Study area

The study was conducted from April 1999 to October 2002 at the Ñacuñán Biosphere Reserve (12,800 ha), 200 km southeast of Mendoza city, Argentina (34°02′S, 67°58′W), and in a surrounding area grazed by cattle. The study area is located in the central portion of the Monte Desert, where the climate is semiarid and seasonal, with hot humid summers and cold dry winters (Guevara et al. 1996). Mean annual precipitation is 347.51 mm (1972–2002 period) and average temperatures (1972–2002) range from less than 10 °C in July to more than 20 °C in January. Since 1997 onwards rainfalls reached values higher than the average, the years of the study being consequently quite humid (fluctuating from 415 to 585 mm).

The vegetation in the area is xerophytic, and several plant communities can be distinguished (Roig 1971; Roig and Rossi 2001), with the most representative ones being the mesquite forest, the creosotebush community and the sand dunes. These three habitat types are present in both the protected and the adjacent grazed area. The mesquite forest and creosotebush are the most heterogeneous habitats (Corbalán and Ojeda 2004). The mesquite forest consists of a tree layer of *P. flexuosa*, accompanied by shrubs of *Larrea divaricata* and a low cover of grasses, whereas the creosotebush community is dominated by shrubs of *Larrea cuneifolia* and a high cover of herbs. Sand dunes are the least heterogeneous habitat, characterised by a low cover of shrubs and a high percentage of bare soil (Roig 1971; Corbalán and Ojeda 2004).

The reserve is embedded within a matrix strongly affected by the main regional activity, i.e. cattle ranching. Livestock is a disturbance agent that may directly influence arid ecosystems in numerous ways, including consumption of plants, redistribution of nitrogen and plant seeds, trampling of vegetation and soil compaction (Beever et al. 2003). The livestock intensity (measured as the number of feces in 100 sampling unities of 16 m² into each habitat type) is greater in the creosotebush community (6.63 ± 3.44), followed by the mesquite forest (5.45 ± 2.68) and the sand dunes (4 ± 2.12) (Tabeni, unpub. data).

A total of 16 sampling sessions in the protected area and 8 sampling sessions in the grazed area were conducted, with each sampling period consisting of 3–7 consecutive nights. Live traps for mammals under 100 g were arranged in two grids of 7×7 configuration (0.81 ha) during the first 2 years (period 1: 1999–2000) in each habitat in the protected area, and in four grids of 5×5 configuration (0.16 ha) during the last 2 years (period 2: 2001–2002) both in the protected and the grazed area.

The small mammals studied were *E. typus*, *C. musculinus*, *A. molinae* and *G. griseoflavus*

(Rodentia: Muridae) (Tab. 1). Traps were baited with rolled oats and checked in the early morning. Captured animals were sexed, weighed, marked and released at the site of capture. In order to recognise optimal and suboptimal habitats for each species across all three habitats and between treatments (protected and grazed area), we estimated sex ratio during the reproductive season (Lidicker 1995) as well as demographic parameters highly correlated to fitness (Diffendorfer 1998).

No previous data on age classes of these species were available, so we established them based on the body mass of individuals (Tab. 2). Those animals showing that they were in reproductive condition (scrotal testes or evident mammary glands) and those lacking these characteristics, but with the same or higher weight, were considered to be adults. As juveniles are generally subordinate to adults, one might expect optimal habitats to present a high abundance of adults compared to juveniles, and vice versa for suboptimal habitats (Van Horne 1982). We compared the adult/juvenile ratio for each species within each treatment using a binomial test, and among habitats using a χ^2 test.

As the breeding season was unknown for most species in the area, we estimated it by analysing the number of reproductive individuals (males and females) in each season using Generalised Linear Models (GLM; McConway et al. 1999). Data were standardised by the number of total trap-nights for each sampling period. As data had a binomial distribution (number of reproductive individuals/ trap-nights), a logistic regression was performed. The season when reproductive animals were statistically more abundant was assumed to be the "breeding season".

As sex ratio can favour females in higher quality habitats during the reproductive season (Lidicker 1995), we calculated the proportion of adult males and females in each habitat type during this season using a binomial test (Siegel 1991). This test was performed when observed values were higher for females than for males.

The numbers of reproductive adult females during the breeding season were compared among habitats and treatments using GLM (logistic regression), and χ^2 as a measure of fit. Trap-nights were used to standardise data because of the unequal number of trapping sessions, and grids were used as replicates. When the residual errors in the analysis showed overdispersion (i.e., the variance of residuals was significantly higher than that predicted by the binomial distribution), data were rescaled to correct for biases in the statistical test of hypotheses (Crawley 1993), and F tests were used instead of χ^2 as a measure of fit.

Due to the low recaptures of individuals over successive trapping sessions, we were not able to analyse survival using Jolly Seber models because their reliability declines when population sizes are very low and/or no marked animals are captured (Sullivan et al. 2000). Instead, we used indirect measurements such as residents versus transients (captured during two or more sessions or only once, respectively), days between first and last capture, and number of trapping sessions in which each individual was captured (Sanchez-Cordero 1993; Loeb 1999; Gundersen et al. 2001).

Table 1. Habitat preferences and ecomorphological attributes of small mammal species of the Monte Desert. *Source*: 1. Campos et al. (2001); 2. Corbalán and Ojeda (2004); 3. Corbalán, (2005); 4. Giannoni et al. (2005); 5. Gonnet and Ojeda (1998); 6. Mares, (1973); 7. Taraborelli et al. (2003).

	Eligmodontia typus	Graomys griseoflavus	Calomys musculinus	Akodon molinae	Source
Body mass (g)	17.5	55.8	22.2	37.2	3
Habitat use	Sand-dunes, open areas; low shrub cover. Nests and retreats underground	Mesquite forest, creosote bush; high shrub cover	Creosote bush; high forb cover	Creosote bush, mesquite forest; high forb cover	2, 5, 6
Locomotion	Quadrupedal/ saltatorial during escape	Scansorial. Quadrupedal/ saltatorial during escape	Cursorial, quadrupedal	Cursorial, quadrupedal	7, 4
Food preferences	Omnivore (tendency to granivory)	Herbivory (strong tendency to folivory)	Omnivore (tendency to granivory)	Omnivore (tendency to insectivory)	1

Table 2. Age classes of each species based on the body mass (g) of individuals

	Akodon molinae	*Calomys musculinus*	*Eligmodontia typus*	*Graomys griseoflavus*
Newborn	$\leqslant 14.9$	$\leqslant 8.9$	$\leqslant 8.9$	$\leqslant 15.9$
Juvenile	15–24.9	9–14.9	9–13.9	16–38.9
Adult	$\geqslant 25$	$\geqslant 15$	$\geqslant 14$	$\geqslant 39$

Table 3. Significance of the "Treatment" (protected/grazed area), the "Habitat" (mesquite forest, creosotebush community and sand dunes) and the "Treatment*Habitat" interaction on the reproductive females along the study period, based on GLM

	Deviance	df	F	P	R^2 (%)
Akodon molinae					
Treatment	6.41*	1–24		0.011	13.20
Habitat	14.93*	2–24		< 0.001	30.76
Interaction	8.39*	2–24		0.015	17.29
Calomys musculinus					
Treatment	1.78	1–24	1.23	0.279	3.06
Habitat	13.83	2–24	4.78	0.018	23.76
Interaction	7.86	2–24	2.72	0.087	13.50
Eligmodontia typus					
Treatment	8.55	1–24	2.90	0.101	7.43
Habitat	29.14	2–24	4.94	0.016	25.32
Interaction	6.68	2–24	1.13	0.339	5.80
Graomys griseoflavus					
Treatment	9.38	1–24	5.43	0.028	15.66
Habitat	7.84	2–24	2.27	0.125	13.09
Interaction	1.28	2–24	0.37	0.694	2.14

*This value corresponds to χ^2 value.

The analyses of survival data were separated between periods 1 (first 2 years) and 2 (last 2 years) because the animals captured in period 1 were not recaptured during period 2, and the trapping grids established were not the same for both periods. One-way ANOVA was performed to analyse the number of trapping sessions in which each individual was captured within the protected area in period 1, whereas two-way ANOVA was used to compare this parameter between treatments and among habitats in period 2.

Results

A total of 11,836 trap-nights were conducted in period 1 (only in the protected area), and in period 2 an equal number of trap-nights (12,700) were set in both the protected and the grazed area. A total of 564 individuals of *G. griseoflavus*, 560 of *A. molinae*, 457 of *E. typus* and 339 of *C. musculinus* were captured throughout the duration of the study. Species abundances for each treatment and habitat type are reported in table 3.

Juvenile/adult relationship

On comparing the proportion of adults and juveniles within each treatment, we found that adults were more frequently caught in both the protected and the grazed area ($P < 0.001$ for all species). Comparing this relationship among habitats, we found that in the protected area adults of *E. typus* were

more abundant in the sand dunes and juveniles in the creosotebush ($\chi^2 = 10.86$: df = 2; $P = 0.004$). In the grazed area, adults of *A. molinae* were more frequent in the creosotebush ($\chi^2 = 5.9$; df = 2; $P = 0.052$).

Breeding season and sex ratio

The breeding season for *A. molinae* and *G. griseoflavus* was spring (October and early December, $F = 40.46$; df = 3–30; $P < 0.001$, and $F = 37.22$; df = 3–32; $P < 0.001$, respectively), with the proportion of reproductive individuals reaching 68% for *A. molinae* and 57% for *G. griseoflavus* in this season. A higher proportion of reproductive individuals of *E. typus* was found in spring and summer (February) (59%; $F = 5.30$; df = 3–24; $P = <0.01$). No differences among seasons were found for *C. musculinus* ($F = 1.49$; df = 3–24; $P = 0.242$), but we considered all seasons except winter (July and August) as the breeding period for this species because no reproductive individuals were found in this season, while 29.5% were found in summer, 29.5% in autumn (April and May) and 41% in spring.

The proportion of adult females to males did not show significant differences during the reproductive season in any habitat ($P > 0.05$ for all species).

Reproductive females

Comparing reproductive females, the treatment (protected/grazed) was significant for *A. molinae* and *G. griseoflavus*. Reproductive females of both species were more abundant in the protected area (85.29% and 86.36%, respectively).

Habitat preference was significant for *A. molinae*, *E. typus* and *C. musculinus*. The reproductive females of *A. molinae* were more abundant in the mesquite forest and creosotebush community (94.1%), whereas *E. typus* and *C. musculinus* had more reproductive females in sand dunes (74.4%) and in the creosotebush community (62.2%), respectively.

The "Habitat by Treatment" interaction was significant only for *A. molinae* (Tab. 3).

Survival

Due to the low number of recaptures in successive trapping sessions, the transient vs. resident relation favoured transients in all cases (Tab. 4). Therefore, we were not interested in making a statistical comparison of this relation, since only resident individuals are indicative of habitat quality. On considering only resident individuals we observed that, in general, habitats within the protected area had more residents than the grazed area. Figure 1 shows that, during period 1 in the protected area, *A. molinae* residents were more frequent in the creosotebush community, whereas the number of *G. griseoflavus* residents was higher in the mesquite forest, and resident individuals of *E. typus* were in the sand dunes. During period 2 in the protected area, *A. molinae* residents also were more frequent in the creosotebush community. Instead, the same number of *G. griseoflavus* residents was found in all three habitats and only one resident individual of *E. typus* was found in sand dunes. All resident individuals of *C. musculinus* were found in the mesquite forest and creosotebush community in both periods 1 and 2, but no individual was recaptured during different sampling sessions in the sand dunes.

In the grazed area, *A. molinae* residents were found in the creosotebush community and mesquite forest in a higher proportion than in sand dunes, *C. musculinus* residents were present only in the creosotebush community, and resident individuals of *E. typus* in sand dunes. *Graomys griseoflavus* showed resident individuals in all three habitats.

Days between first and last capture are given in table 3 as maximum and median values. Except for *C. musculinus*, the maximum number of days of residence was recorded in the protected area, and the higher median values were also found in the protected area (period 1), but for all species.

The mean number of trapping sessions in which each individual was captured is shown in table 3. One-way ANOVA revealed that no species showed differences in the number of trapping sessions among habitats over the first 2 years. Two-way ANOVA indicated

Table 4. Survival measurements for each small mammal species during period 1 (first 2 years) and period 2 (last 2 years) of trapping sessions in the protected area, and in the grazed area

| Treatment/period	Species	Habitat	Residents	Transients	Trapping sessions	Days (Max)	Days (Med.)
Protected area (period 1)	Akodon molinae	Creosotebush	18	72	1.23 ± 0.50	345	195
		Mesquite forest	5	34	1.13 ± 0.34	345	195
		Sand dunes	0	4	1.00 ± 0.00	—	—
	Calomys musculinus	Creosotebush	4	64	1.09 ± 0.41	255	145
		Mesquite forest	3	22	1.12 ± 0.33	190	190
		Sand dunes	0	17	1.00 ± 0.00	—	—
	Eligmodontia typus	Creosotebush	6	44	1.12 ± 0.33	125	77.5
		Mesquite forest	4	28	1.16 ± 0.45	105	72.5
		Sand dunes	13	96	1.12 ± 0.32	200	190
	Graomys griseoflavus	Creosotebush	16	37	1.38 ± 0.63	345	77.5
		Mesquite forest	14	51	1.31 ± 0.66	510	102.5
		Sand dunes	1	9	1.10 ± 0.32	85	85
Protected area (period 2)	Akodon molinae	Creosotebush	36	71	1.42 ± 0.67	276	93.5
		Mesquite forest	7	31	1.31 ± 0.74	238	147.5
		Sand dunes	11	27	1.37 ± 0.67	373	96
	Calomys musculinus	Creosotebush	3	40	1.09 ± 0.37	129	101
		Mesquite forest	3	18	1.19 ± 0.51	169	96
		Sand dunes	0	13	1.00 ± 0.00	—	—
	Eligmodontia typus	Creosotebush	0	6	1.00 ± 0.00	—	—
		Mesquite forest	0	6	1.00 ± 0.00	172	172
		Sand dunes	1	18	1.05 ± 0.23	69	69
	Graomys griseoflavus	Creosotebush	8	60	1.15 ± 0.46	244	91
		Mesquite forest	9	51	1.17 ± 0.42	239	100.5
		Sand dunes	8	43	1.21 ± 0.64	151	96
Grazed area	Akodon molinae	Creosotebush	9	31	1.22 ± 0.42	92	88
		Mesquite forest	11	52	1.21 ± 0.50	287	105
		Sand dunes	4	29	1.18 ± 0.53	173	134
	Calomys musculinus	Creosotebush	2	19	1.09 ± 0.30	368	90
		Mesquite forest	0	17	1.00 ± 0.00	74	61.5
		Sand dunes	0	8	1.00 ± 0.00	—	—
	Eligmodontia typus	Creosotebush	0	8	1.00 ± 0.00	130	91
		Mesquite forest	0	8	1.00 ± 0.00	—	—
		Sand dunes	2	21	1.09 ± 0.29	150	69
	Graomys griseoflavus	Creosotebush	6	40	1.15 ± 0.42	180	91
		Mesquite forest	8	46	1.17 ± 0.42	250	98
		Sand dunes	5	35	1.17 ± 0.50	149	81
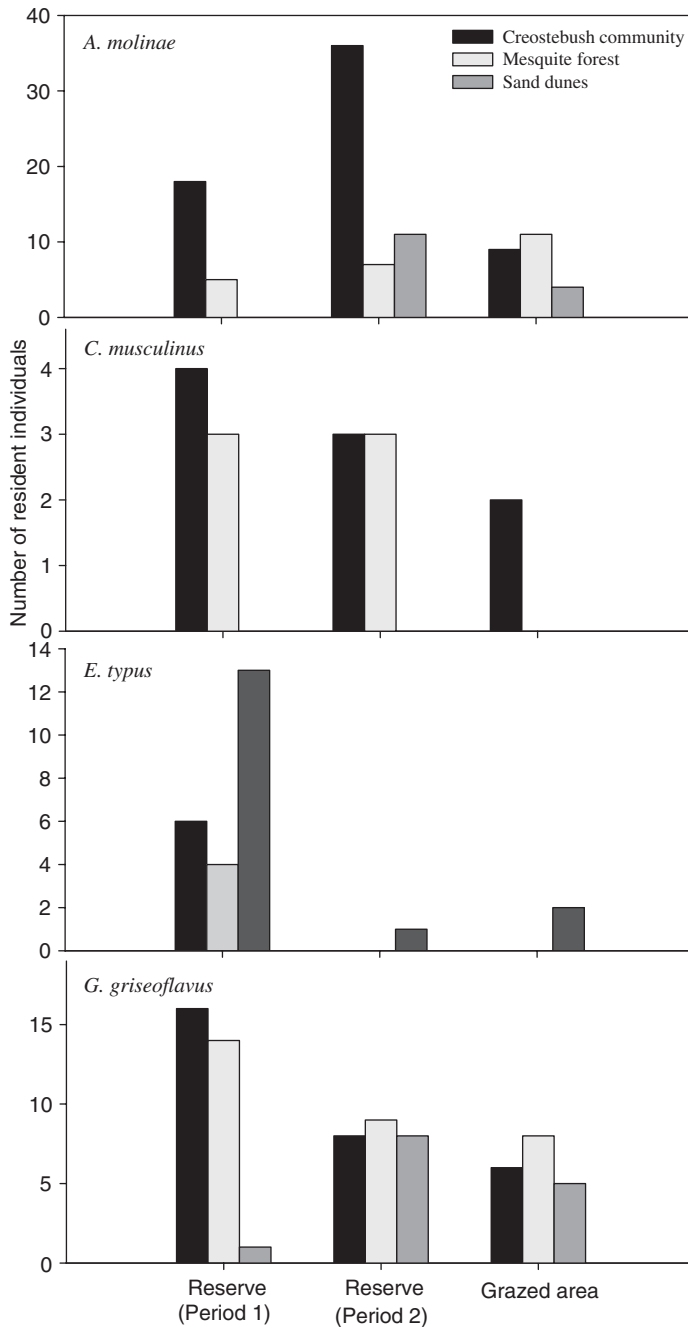
Fig. 1. Number of resident individuals in the reserve (periods 1 and 2) and grazed area for each small mammal species.

that only *A. molinae* showed higher persistence in the protected area ($F = 4.84$; $df = 1$; $P < 0.05$) in the last 2 years.

Discussion

Previous studies on habitat selection conducted in the Monte Desert in recent years demonstrated that habitat is an important factor in determining the spatial distribution and community structure of small mammals (Ojeda 1989; Gonnet 1998; Gonnet and Ojeda 1998; Corbalán and Ojeda 2004; Tabeni and Ojeda 2005). Plant cover provides safe places to avoid predation, especially for *C. musculinus*, *A. molinae* and *G. griseoflavus*. Selection of closed microhabitats is a shared attribute with quadrupedal and nocturnal species from the North American, Asian and African deserts (Brown et al. 1992). The morphological features of *E. typus* (elongated hind legs, erratic escape behaviour, hairy cushions on the soles of its feet) allow this species to exploit more open areas (Taraborelli et al. 2003). On our study site, the reserve is a higher density area for *A. molinae*, and so is the grazed area for *E. typus* (Tabeni and Ojeda 2005). At habitat level, *C. musculinus* and *A. molinae* show higher densities in the creosotebush, whereas *E. typus* is dominant in the sand dunes (Corbalán and Ojeda 2004; Tabeni unpl. data). *Graomys griseoflavus* is a habitat generalist that has no marked preferences for any habitat type, although it is the dominant species in the mesquite forest (Corbalán 2004). In the current study, we analysed fitness-related parameters to infer optimal and suboptimal habitats for each species, and to evaluate whether previously reported densities could be indicators of habitat quality in this community.

We analysed the responses of the species under investigation at two levels. The first level was between treatments: protected and grazed areas. The second level was among habitats: mesquite forest, creosotebush community and sand dunes.

At the first level, we found that the protected area was in general better than the grazed area. *Akodon molinae* and *G. griseoflavus* showed a higher proportion of reproductive females and higher survival in the protected area. It appears that disturbance generated by cattle affect these species as they reduce plant cover as well as available refuges to avoid predators. *Calomys musculinus* and *E. typus*, instead, showed no preferences between treatments. At the second level (among habitats) we found that the creosotebush community and the mesquite forest are the best habitats for *A. molinae* and *C. musculinus* because proportion of reproductive females and survival were higher in them. Highly heterogeneous habitats like these have a greater availability of safer microhabitats (Rosenzweig and Winakur 1969; Holbrook 1978; August 1983) and this could explain the higher fitness of cursorial species found in there. *Graomys griseoflavus* had more resident individuals in the mesquite forest, but the rest of the parameters showed no differences among habitats, probably due to this species' higher plasticity to occupy different habitats and to its abilities to avoid predators. *Eligmodontia typus*, instead, had higher fitness in sand dunes, as was demonstrated by several parameters (proportion of reproductive females, adult proportion, survival). Its morphological attributes and the absence of competitors in open areas could explain why sand dunes are considered as an optimal habitat for this species.

Some parameters (such as proportion of reproductive females, age ratio, and survival) give us valuable information about the quality of the habitat. According to our predictions, better-quality habitats correlate with a higher density in each murid species. Sex ratio, instead, was not a good estimator of habitat quality in the studied community. Although in deserts annual rainfalls determine ecosystem productivity and consequently food availability, it appears that in the study area this phenomenon affects habitat quality in the same way, since species abundance varies among seasons of the year, but habitat preferences are maintained. Higher densities occur in autumn in all three habitats, probably because of the recruitment of juveniles born in months of high food availability (spring–summer) (Corbalán 2004; Corbalán and Ojeda 2004; Tabeni unpub. data).

In contrast to studies on other species, in this study we demonstrated that, for the murid species in the central portion of the Monte Desert, density is a good indicator of habitat quality. Identification of better and poor habitats provides a valuable input since this area is, and has been for the past decades, highly exposed to degradation. This has implications for the understanding of community structure and local co-existence, as well as for management and conservation programmes.

Acknowledgements

Zusammenfassung

Habitatqualität für vier Kleinsäugerarten der Monte-Wüste, Argentinien

Aufgrund klimatischer und menschlicher Einflüsse findet sich in den temperaten Wüsten von Südamerika ein vielfältiges Landschaftsmosaik. Im zentralen Teil der Monte-Wüste koexistieren vier Kleinsäugerarten (*Eligmodontia typus*, *Calomys musculinus*, *Akodon molinae* und *Graomys griseoflavus*), die aber unterschiedliche Habitatpräferenzen zeigen. Drei wichtige Habitattypen kommen im Untersuchungsgebiet vor: Mesquite-Gebüsch, Larrea-Gebüsch und Dünen.
Die vorliegende Studie quantifiziert die Habitatqualität für die vier genannten Arten in einem Schutzgebiet (Reserve MAB Ñacuñán) sowie angrenzenden Weiden durch demographische Parameter. Diese Parameter korrelieren mit der Fitness im jeweiligen Habitat bzw. Nutzungstyp.
Ganz allgemein zeigt das Schutzgebiet eine bessere Habitatqualität als die beweideten Flächen (insbesondere für *A. molinae* und *G. griseoflavus*). Lokal fanden wir eine größere Fitness von *A. molinae* und *C. musculinus* im Mesquite- und Larrea-Gebüsch als in der weit weniger komplexen Sanddüne. Für *E. typus* dagegen erwiesen sich die Sanddünen als optimales Habitat für Überleben und Reproduktion.

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